COMMENTS ON "EVALUATION OF CAUSES FOR THE DECLINE OF THE KARLUK SOCKEYE SALMON RUNS AND RECOMMENDATIONS FOR REHABILITATION," BY R. VAN CLEVE AND D. E. BEVAN

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The causes for the decline of the Karluk River sockeye salmon runs are many and diverse. Van Cleve and Bevan oversimplify the case, stressing but a few factors and ignoring others without adequate explanation of their omission. Their paper also contains several obvious misstatements, e.g.,

> Rounsefell in 1958 was apparently unaware of the work of the International Pacific Salmon Fisheries Commission on the Fraser River sockeye that had revealed the peculiar life history of several of the largest runs in that system which spawn below the lakes where the young are reared so that the fry have to migrate upstream into the nursery lakes . . . .

In my report (Rounsefell, 1958:85), I specifically refer to this habit in the sockeye salmon that spawn below both Chilco Lake and Babine Lake. On the same page I refer to Philip Nelson observing the young of these river spawners at Karluk working upstream through the weir pickets. This habit was well documented long before the Salmon Commission existed.

Again they state,

> . . . there is now no reason for support of Rounsefell's assumption that all segments of the run interbreed, i.e., that escapement from any part of the run is equally desirable.

On page 147 of my report I state,

> . . . . On the average, neither the very early nor the very late spawners are as successful as those spawning in midseason. The analyses showed that because of the deleterious effects on survival of low autumn (11 out of 48 years) and late spring (about 14 out of 47 years) temperatures, survival depends to some extent on the season of spawning. It would be best then to abandon the idea of obtaining a spring and fall group of spawners, but rather to encourage the canning of the early and late fish, and insist on a higher percentage of the summer fish being in the escapement. . . .

They state that the estimate of 400,000 sockeye salmon spawning in Karluk River in 1926 is " . . . more fish than were recorded for any other part of the watershed." If the 400,000 is compared with the 1926 escapement of 2,500,000 it comes to only 16% compared with 84% in the lake and its tributaries. I assume that Van Cleve and Bevan are not trying to say that while those that enter the lake consist of a large number of subpopulations, the river spawners are only one subpopulation. If they do mean this they obviously invalidate their comments about the Birkenhead River spawners consisting of different races spawning along the same stream at different distances from its mouth. Rich (Gilbert and Rich, 1927:23) states on 18 July 1926 that

> . . . . Any estimate of the number of spawning fish was difficult but it was thought that certainly not less than 300,000 fish, and probably about half a million, had entered Upper Thumb River up to this time.

This was far too many spawners for the exceptionally dry year of 1926, and the returning progeny numbered only 1,460,000. This can be compared with the 1931 escapement of only 870,000 which produced a return of 2,600,000, with but 22% of summer spawners.

Van Cleve and Bevan also state,

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A measure of the small importance attached to the Karluk [River] spawners is that all reports including Gilbert and Rich (1927) do not include the Karluk River on their maps of the watershed.

To this one might reply that neither do the available manuscript reports of the junior author (Bevan and Walker, 1955; Bevan, 1957) or the unpublished manuscript reports of W. F. Thompson (Thompson, 1951; Thompson, Bevan, and Thorsteinson, 1954; Thompson and Bevan, 1954) include the river on their maps. The map in my report (Rounsefell, 1958) does show the river, just as does that of Van Cleve and Bevan. As a matter of far more importance, I do not find any attempt to measure the number of sockeye spawning in the Karluk River in any of the manuscripts just mentioned. My report, showing that in some years a number of mid- to late-season sockeye salmon spawned in the river below the lake, apparently stimulated the authors into hypothesizing one cause for the decline of the runs. In this connection I should like to mention that Bevan and Walker (1955) tabulate the results of their Karluk sockeye salmon spawning ground observations in 1954. They total 138 observations (101 by Bevan and Walker themselves) between 18 May and 29 September. Very surprisingly not a single observation is recorded for the Karluk River despite the fact that they camped at the weir site at the foot of the lake.

Van Cleve and Bevan attempt to explain the importance of the Karluk River spawners by saying that the river spawners were predominately of age 5_3 and that their decline in numbers could explain the increase in relative numbers of 4-yr smolts in the total runs. An examination of the basic data on which they base their conclusions (Barnaby, 1944) finds (Figure 1) that for the brood years 1922 and 1924 through 1929 that the rate of decrease of the 5_3 age group is similar in both the spring and summer-fall groups of spawners. The latter group of spawners, with the slightly greater decrease in the 5_3 age group shows a somewhat higher rate of return, quite the contrary of the theory advanced by Van Cleve and Bevan concerning the superiority of the 5_3 spawners.

The assumption of two seasonal modes in the Karluk run (or merely one mode depleted in the center as these authors claim) is not borne out by the weekly data on runs accumulated since 1921. Thus in the 30-yr period from 1921 through 1950 (Rounsefell, 1958; see also Figure 2) three modes are evident. The first mode, peaking in mid-June, falls off rapidly with a low point in the week ending 12 July. The second mode peaks from the first to the ninth of August. The second low point is not as distinct as the first because of overlapping between the second and third modes but it is about August 16th. The third mode peaks in

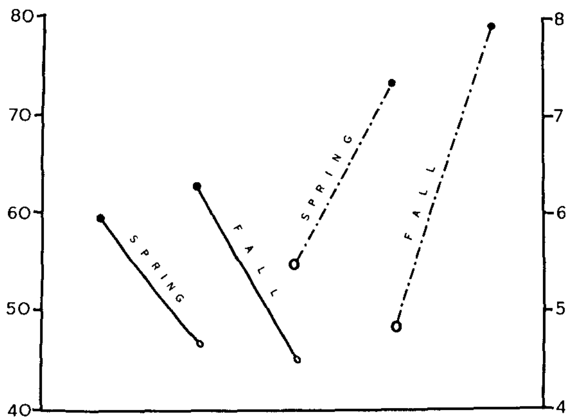

FIGURE 1.—Relation of age 5_3 fish to brood years and return date (Barnaby, 1944). Showing the geometric mean (left hand scale) of the percent 5_3 age fish in the spring and fall runs (solid lines). Dots are for the spawners, open circles for the returns. Geometric mean of number (-00000) of spawners (dot-dash lines) in brood years (open circles) and geometric mean of number in returns (dots).

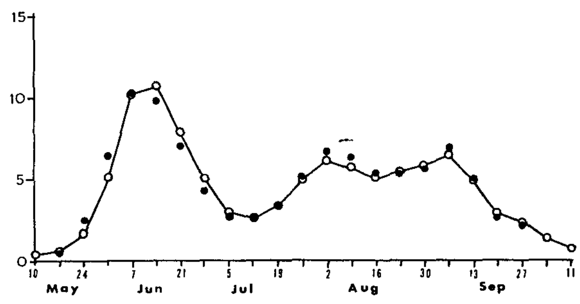

FIGURE 2.—Percentage seasonal occurrence of the Karluk sockeye salmon runs 1921-50 (open circles) and percentage seasonal occurrence of age 5_3 fish 1922 and 1924-49 (dots).

early September. Van Cleve and Bevan cite Walker and Bevan (1955),[2]

> . . . . They also maintained that the decrease in Karluk River spawning could explain the increase in relative numbers of 4-yr smolts, since the river spawners were predominantly of 5_3 age.

To refute this claim one has only to look at Figure 2 showing the seasonal occurrence of the total runs and of the 5_3 age group during the 30-yr period in which this alleged reduction in Karluk River spawners was supposed to have taken place. In other parts of their paper they state that the center of the run, which they claimed spawned in the main river, was supposed to have been depleted before 1921; you cannot have it both ways. Very obviously the decrease in the proportion of fish of 5_3 age has been occurring almost equally in all segments of the runs.

The authors place undue emphasis on a quotation from Chamberlain (1907), which they suggest proves that in the early years there was only one peak in the run. As I shall mention later, Cloudsley Rutter actually said that there were two runs, but that only one occurred in the year (1903) he visited the lake. Chamberlain was not personally acquainted with Karluk but was paraphrasing field notes by Rutter. In discussing the egg take of the Karluk hatchery for 1898 (the parent brood year for most of the 1903 run described in Rutter's notes) Moser (1901:342) says,

> Of the season's take the spring run therefore amounted to 50.4 per cent as against 49.6 per cent for the fall run . . . . the monthly percentages of fish spawned are as follows: June, 0.5 per cent; July, 47.9 per cent; August, 2.9 per cent; September, 41.5 per cent; October, 6.8 per cent; November, 0.4 per cent.

In discussing the hatchery operations for 1899 Moser (1901:343) lists the eggs taken as coming from the spring run and from the fall run. Again, on page 344 Moser states,

> It would appear from the above that the eggs eye very much faster with the spring run, and that the hatching range covers a much longer period. It is also apparent that in considering the hatching of redfish at Karluk the two runs must be treated separately—*the runs are so marked* and the prevailing conditions so radically different . . . . the early run in 1899, under natural conditions of temperature, hatched in an average of 129 days, whereas the fall run required 198 days. [Italics mine.]

The constant reiteration by Van Cleve and Bevan of the notion of a former run with only one mode is quite contrary to their insistence that the run consists of subpopulations and that only the main river spawners are of any importance in maintaining the run.

If we concede for the moment that there are strong tendencies for most sockeye salmon to attempt to spawn in their natal area (within reasonable limits), then we can make a separate assessment of the relative reproductive success of different portions of the run. For the 25-yr period from 1921 to 1945 I have compared the spring, summer, and fall escapements (only spring escapement was available for 1934) with the size of the run returning 5 yr later during the same respective seasons. The resulting returns per spawner for all three periods (73 comparisons) are shown in Figure 3. Table 1 shows which of the three groups of spawners was most successful for the same number of spawners, and on odd- and even-numbered years.

This table shows that if the theory of independent seasonal subpopulations at Karluk advanced by Van Cleve and Bevan is correct, the spring and summer spawners are about equally successful; the fall spawners are much less successful. It also shows that fall spawners, while successful on the odd-numbered years, are very unsuccessful on the even-numbered years. This analysis therefore strongly suggests that it is chiefly the fall spawners (not the summer spawners as Van Cleve and Bevan contend) that use the main river and are thus in direct competition with the large even-year pink-salmon, *O. gorbuscha*, runs.

Concerning the question of races and seasonal races I should like to emphasize the lack of factual data in the report of Van Cleve and Bevan. They quote liberally and at length from various unpublished manuscripts and inhouse mimeographed memoranda. Thus they cite an unpublished manuscript by Gard and Drucker

[2] Walker, C. E., and D. E. Bevan. 1955. Observations on the biology of the red salmon in the Karluk watershed. Unpubl. manuscr. Univ. Wash., Fish. Res. Inst., Seattle, WA 98195.

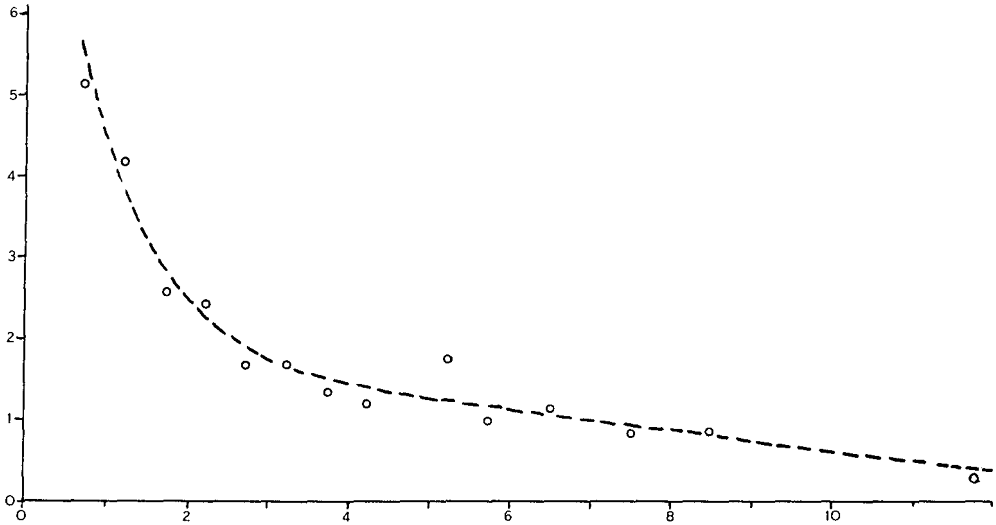

FIGURE 3.—Ratio of returns to number of spawners for the spring, summer, and fall groups of spawners (see text) on the ordinate scale against hundreds of thousands of spawners (abscissa).

TABLE 1.—Showing the number of odd- and even-numbered years on which each group of spawners produced returns falling above or below the curve of Figure 3.

Spawning group	Odd years			Even years			All years		
	Above	Below	Percent above	Above	Below	Percent above	Above	Below	Percent above
Spring: to 21 June	6½	6½	50	7	2	78	13½	8½	61
Summer: 22 June-16 Aug.	9½	3½	73	4½	6½	45	14	10	58
Fall: 17 Aug. on	6	7	46	1½	8½	15	7½	15½	33
All seasons	22	17	56	13	17	43	35	34	51

(1972)[3] and say (data not given) that Gard and Drucker demonstrated the existence of these races by comparing early spawning sockeye salmon in the lateral tributaries of the lake, in the upper Thumb, O'Malley River, and Canyon Creek with later spawners in these terminal streams, and on the Thumb Beach in Karluk Lake. The late spawners were said to show greater mideye to fork length, and greater fecundity at comparable lengths.

According to this statement Van Cleve and Bevan show, not a comparison between geographical localities (the same localities in each season were not used) but merely between early and late spawners. The validity of the quoted comparison is open to serious question. In my published report on the fecundity of North American Salmonidae (Rounsefell, 1957) I note that for Karluk sockeye salmon, over a 4-yr period, that 60-cm sockeye with 2 yr at sea showed a consistently and statistically significant higher fecundity than Karluk sockeye with 3 yr at sea. These data were for fish running throughout the season.

Davidson and Shostrom (1936:9) showed that late-running salmon have longer heads and that the distance from the eye socket (equivalent to Gard and Drucker's center of the eye for general

[3]Gard, R., and B. Drucker. 1972. Differentiation and cause of decline of sockeye salmon of the Karluk River system, Alaska. Unpubl. manuscr. Auke Bay Fish. Lab., Natl. Mar. Fish. Serv., NOAA, Auke Bay, AK 99821.

anatomical position) to the back of the head in 36 days increased in percentage of body length (measured from the back of the head) by 5.08%. Thus we do not need to postulate races on the basis of the unpublished findings of Gard and Drucker.

If we were to assume (as done by Van Cleve and Bevan) that the early and late spawners in the same tributary are of separate races, then there is no plausible explanation of why large numbers of late-running 4_3 grilse should presage a large total run of 5_3 age fish in the following year, yet the coefficient of correlation between them over a 25-yr period is 0.956 and highly significant. Rich describes these 4_3 grilse (Gilbert and Rich, 1927:32-33),

> A larger size of grilse, belonging to group 3, is one year older than those above mentioned and returns in its second season in the sea as 4-year fish. These are still largely, but not exclusively, males, and are undersized fish of little value . . . . conspicuously deficient in color of flesh and amount of oil, ...

I question the quotation concerning fry from river spawners (the report says it was a 1951 observation but from what field notes or unpublished manuscript is not divulged) in which Walker is purported to state concerning these river-derived fry that,

> . . . . These fish were, on the average, three millimeters longer and had heavier bodies than those *seen* elsewhere. [Italics mine.]

Such a supposedly exact comparison between two or more sets of data without divulging the source is questionable. Did he compare actual measured and weighed samples with fry from spring, summer, or fall spawners in lateral or terminal tributaries of Karluk Lake? Or with beach spawners, or with fry from Thumb or O'Malley Lakes?

Van Cleve and Bevan follow this by stating,

> . . . .Walker and Bevan maintained that since fry from the Karluk River are largest at the time of emergence, they should also be largest at the time of seaward migration if they retain their size difference during lake residence.

This statement apparently infers that biologists should believe that fry from eggs spawned in June are smaller when they emerge from the gravels in the spring than are fry from eggs spawned in the fall. Such a statement requires carefully gathered data for substantiation. It is more likely that if data exists showing smaller fry descending into the lake from tributary streams, the fry were from the late spawners in those streams and that the fry from the early spawners descended into the lake in the very early spring, probably unobserved.

The probability of a very early lakeward migration of the fry from the early spawners is suggested by records of the Karluk hatchery (Moser 1901:345-346),

> According to a report from the hatchery, under date of November 3, 1900, all the June eggs and part of the July eggs had hatched out, producing an excellent lot of healthy fry. It was found (1900) that the earlier eggs and the September eggs were the best, while a portion of those taken during the middle of the season were of indifferent quality. . . .
>
> After the fry are hatched out they escape to the bottom of the trough, ... As they age they require more space, but they are usually held in the parent trough until the egg—or umbilical—sac is absorbed, a period of about ten weeks, depending upon the temperature of the water.

This suggests that the spring fry would be ready to emerge from the gravel of the redd by the middle of January.

At another point Van Cleve and Bevan paraphrase an additional unpublished manuscript by Walker and Bevan saying,

> . . . . Walker and Bevan (1955)[8] noted that the largest spawning population of sockeye salmon in the Karluk watershed was found in the Karluk River.

This type of generalized statement, without presentation of data is unconvincing, especially as in the second paragraph of the whole paper Van Cleve and Bevan used the factor of 10% of the total run to estimate the numbers spawning below the lake in 1971, as determined by the National Marine Fisheries Service in 1963. In fact, it means almost nothing for them to say "largest" when in another place they say 400,000 (out of an escapement of 2,600,000) was "more fish than were recorded for any other part of the watershed."

They quote from the Karluk River report of Gilbert and Rich (1927) a statement by Rich,

> . . . . The spawning escapement [of 1926] was the best in many years, and in all probability was the best that has ever been observed by the few white men who have visited the lake.

They then append the following footnote,

> This was certainly a rhetorical statement with little foundation other than Rich's impression of a "big" run.

Actually Van Cleve and Bevan are wrong. The total run of 1926 was exceeded only by those of 1901 and 1906. The escapement in 1926 of over 2½ million sockeye salmon was certainly larger than in either of the two earlier years. In 1901 for instance the egg take for the Karluk hatchery was less than in all but 7 of the 20 yr the hatchery operated. They admit themselves that despite regulations to the contrary fishermen were still operating in the river itself as late as 1899, and were not officially excluded from the lagoon until 1918. Furthermore, there is no record of anyone visiting Karluk Lake in either 1901 or 1906.

Van Cleve and Bevan have devoted far too much space to trying to prove that my assumption of a 35% escapement before installation of a counting weir in 1921 is much too conservative, apparently in order to substantiate their theory of one large seasonal run overfished in the center. Yet there are no records in existence by which one can make a truly sound estimate and the exact proportion is of little consequence. When one considers, however, the numerous closed fishing seasons that had to be imposed from time to time each year after 1921 in order to achieve a 50% escapement through the weir it is wholly unreasonable to expect more than a 35% escapement in the earlier years of almost unrestricted fishing in the river and the lagoon. They go so far as to credit Gilbert and Rich (1927) as supporting their view (despite their earlier reflections on the validity of Rich's statements), saying,

> A careful reading of Gilbert and Rich (1927) also shows that they felt that Rutter's estimate of the total number that spawned in Moraine Creek in 1903 was about one-half as large as the true figure.

Van Cleve and Bevan perhaps failed to note that Rutter kept a careful count of spawners in Moraine Creek over a full month from 5 August to 5 September. Rutter also stated that in 1903 the spawning season was practically over early in September. Far from supporting the view of Van Cleve and Bevan, Rich says,

> In 1926 Moraine Creek was well seeded by this early run and was also used extensively by the later runs—those that spawned in the early part of August, at the same time Rutter's observations were made. . . . It is quite probable that conditions were vastly different in 1903 than in 1926, and that the early escapement was very much smaller. Certainly, if Moraine Creek in 1903 had received anything like the early spawning run it had in 1926 the remains of the dead fish would have attracted the attention of a well-trained observer such as Mr. Rutter.

In this connection it should be noted that Van Cleve and Bevan also use Rutter's statement (Chamberlain, 1907) to prove that the early years had only one peak in the runs. However, Rutter actually said,

> The Karluk is said similarly to have two runs, one maximum about the last of June and one the first of August, but this was not true in 1903 when the river was under study.

It is thus quite clear that Rutter had been well informed on the usual two runs, the first one being the larger. The use of what happened in only one year (1903) to prove the usual nonexistence of a large early run is poor extrapolation on the part of Van Cleve and Bevan in my opinion.

It should be noted that Van Cleve and Bevan in claiming to believe my admittedly rough assumption of a 35% escapement during the early years of the fishery is too conservative, base their argument partially on the lower return per spawner in the 1929-48 period as contrasted with the earlier period. Nevertheless they have not challenged my calculations (Rounsefell, 1949) showing escapements of sockeye salmon in the Fraser River from 1894 to 1921 as amounting to only 18% of the runs (only 6% in the heavily fished war year of 1917), and its increase to 27.4% of the run in the 1922-45 period of stricter law enforcement and longer closed seasons.

Concerning their theory that in the earlier years of the fishery there were no early or late runs, Van Cleve and Bevan also state,

> . . . . even though Thompson's analysis of the catch in his 1950 paper was based upon that of a single cannery [the actual cannery was not named although the Alaska Packers Association operated three canneries at Karluk and usually did not operate them all for the entire season], it agreed with this earlier observation [referring to Rutter's statement concerning lack of a large early run in 1903, even though Rutter also said that the Karluk is said to have two runs] and *proved that the spring and fall peaks evident in 1921 were artifacts.* [Italics mine.]

My Figure 2 clearly shows that over a 30-yr period the existence of spring, summer, and fall runs was not an artifact, even though the catch was taken from almost exactly the same portion of the seasonal runs as in the earlier years. Why then do they assume that the seasonal runs differed between the two periods? And if, as they state, the midseason fish were so badly depleted by fishing in the earlier years, how was this midseason run, which by their reasoning should have been wiped out, still furnishing the largest share of the catch? It would appear from the actual data on hand that the only "artifact" is their hypothetical large midseason run.

On the point of the weir at the foot of Karluk Lake obstructing the downstream migration onto river spawning areas of some adults in occasional years, I agree with Van Cleve and Bevan that this is undesirable. I went through the same problem in Maine where the hatchery personnel insisted on fish tight weirs below every lake before planting landlocked salmon. They mistakenly thought that the salmon were escaping when they dropped downstream to spawn, often in the only spawning area available. I do not agree that the weir has been any serious obstacle to upstream migrating salmon, but in Karluk with the often enormous pink salmon runs it is difficult to maintain a weir downstream because of the dead carcasses of spawned-out salmon.

This habit of late-running sockeye salmon spawning in an outlet river is well known. The very late salmon may seldom reach the lake. In some rivers the earlier portion of the late spawners may enter the lake until their gonads are ready for spawning and then drop downstream, but I note that even Van Cleve and Bevan do not claim that this is an annual occurrence at Karluk, being able to cite but one instance. There is no good reason, however, why the Karluk weir cannot be easily converted into an upstream and downstream weir.

I do not agree that obtaining most of the escapement in midseason is the panacea. To begin with it appears that the main river spawners (contrary to Van Cleve and Bevan) are recruited chiefly from rather late-running fish. Secondly, the large pink salmon runs in the even years will continue to handicap the even-year river spawners more than those in Karluk Lake tributaries. In their Table 3 Van Cleve and Bevan show a table from Burgner et al. (1969) that shows only 126,000 redd sites in the main river. When such a spawning area is also used by thousands of pink salmon on the even years (Bevan in his 1956 survey shows 700,000 spawning pink salmon actually observed) the competition between pink salmon and late-running sockeye salmon in the main river is obvious. In earlier years the pink salmon runs varied greatly in numbers since insufficient harvesting when the runs were large caused cataclysmic declines in following cycles. Under present conditions of better harvesting of pink salmon runs it would appear unwise to count on good sockeye production from the main river in most even years.

I did point out (Rounsefell, 1958) that after the weir was moved to the lake outlet in 1945 it was discovered that some pink salmon passed into the lake every year, varying from less than a hundred to 16,000 in odd years, and from 37,000 to 87,000 in even years.

Van Cleve and Bevan minimized the spawning areas in Karluk Lake and its tributaries while maximizing the spawning areas below the lake. Thus the table of Burgner et al. (1969) is presented without adequate explanation. Burgner et al. show:

Karluk system	*Hectares*	*Redd sites* (based on 2 m^2)
Terminal streams	1.67	8,000
Lateral streams	6.71	34,000
Lake beaches	1.25	6,000
Outlet river	25.28	126,000
Total	34.91	174,000

The text of the report by Burgner et al., however, says that in the shallow torrential lateral streams in the Karluk system, space requirements were often substantially less than 2 m². They also say their figure is only an approximation complicated by the occurrence of successive waves of spawners in successive streams. They also admit incomplete information on the amount of potential spawning ground, especially on lake beaches, and their figure includes only the beach spawning areas of Thumb and O'Malley Lakes. Observations of beach spawning have been published, mentioning Tent Point, Meadow Point, Cascade Creek, Moraine Creek, Canyon Creek, Halfway Creek, off Boulder Point, off Grassy Point Creek, etc.

Fred Lucas estimated in 1924 that sockeyes spawning in O'Malley River would average a pair to each square yard. (Gilbert and Rich, 1927:20).

The estimate of the area (Burgner et al., 1969) of river spawning beds is quite meaningless in my opinion without information on the location of these beds along the 30-mile course of the Karluk River. Furthermore, in the estimates of main river spawning areas for other systems redd sites range from 3 to 8 m² rather than the 2 m² used for Karluk.

Burgner et al. (1969:457) also say,

> The individual spawning areas in the Karluk system are occupied continuously for about 5 weeks to 5 months by a succession of spawners, with the result that many more spawners are accommodated than could be if they all spawned in 2 or 3 weeks. This occupation by successive waves of spawners introduces questions as to the effect of superimposition of redd sites on the success of spawning. *We do not know the answers.* [Italics mine.]

Since the sources of Van Cleve and Bevan's spawning area data readily admit that they do not have the answers to many of the questions raised in attempting to convert spawning area into redd sites, I believe that their figures need considerable qualification and cannot be taken seriously.

From the above discussion I suggest that the number (ignoring the main river since there is no locality information given) of redd sites would be more like the following:

Terminal streams	32,000
Lateral streams	144,000
Lake beaches	60,000
Total	236,000

That is, the lake and its tributaries should, have, and can accommodate about half a million spawners without overcrowding.

It is apparent that the Karluk sockeye salmon run is continuing the decline that was accelerated by destruction, since 1921, of the natural cyclic character of the runs. Restoration of the runs at this stage can scarcely be expected from merely assuring a more even seasonal distribution of spawners.

Two important factors I stressed 15 yr ago were the control of both density-dependent and density-independent predators in order to raise the number of smolts per spawner leaving the lake, and hopefully to raise the biomass of smolts in the lake to a level where eventually it would lower the threshold size of the migrating smolts, so that we would have a reversal of the trend toward more 4-yr and fewer 3-yr smolts.

In this regard I note that Van Cleve and Bevan refrain from mentioning the high mortality of spawning salmon by Kodiak bears. Shuman (1950) reported a bear kill of unspawned salmon of 94,000 or 19.4% of the 1947 spawning escapement of 485,000. If this quantity has been lost annually since I recommended control 15 yr ago it means a loss of 1,400,000 spawning salmon.

I also recommended (Rounsefell, 1958) that an attempt be made to restore the cyclic character of the runs, stating,

> The attempt to stabilize the runs by obtaining a high number of spawners in every year has largely destroyed and obscured the former cyclic character of the runs. During the period when these cycles were present the number of spawners fluctuated in a more or less regular manner from very high to very low (lower than most recent years). This wide variation in number of spawners resulted in wide oscillations in the numbers of young sockeye present in the lake and therefore available as food for predator fishes. These regular oscillations in the supply of available prey may have acted as a control on the abundance of predators.

I then explained more fully its purpose as follows:

. . . by restoring insofar as practicable the former cyclic character of the runs in order to lessen competition between the older young and fry, and perhaps give some measure of natural control of predators. Because of the present low state of the runs this should be accomplished by providing a higher proportion of spawners on big runs rather than by decreasing the proportion on smaller runs, ...

This recommendation was concurred in by Thompson, Bevan (junior author of the present paper), and Thorsteinson (1954) in which they state,

The assumption is made, under this quota system, that by allowing a larger escapement in poor years, these years can be built up to a level of good years. This is probably in error. Poor cycle years are now known to be due to natural conditions which limit production and attempts to rebuild these poor years in Bristol Bay and elsewhere by radical restrictions have failed . . . . The cycles in the Karluk and elsewhere seem to have broken down, possibly due to efforts to increase escapement ratios in poor years, thus probably destroying natural conditions favorable to the big-cycle years.

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